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Title

Size-dependent foraging niches of European Perch *Perca fluviatilis* (Linnaeus, 1758) and North American Yellow Perch *Perca flavescens* (Mitchill, 1814)

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Abstract

Body size of consumer species is a fundamental trait that influences the trophic ecology of individuals and their contribution to the functioning of freshwater ecosystems. However, the relationship between body size and trophic ecology can be highly variable both within and between closely-related and similarly-sized species. In this study we compared the intra- and interspecific relationship between body size and trophic position for North American Yellow Perch *Perca flavescens* and European Perch *Perca fluviatilis*, which share similarities in morphology, life history traits and trophic requirements. We used stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) to characterize differences in size-dependency of trophic position and to trace consumer foraging history of Yellow Perch in lakes in the Northwestern United States and European Perch in lakes in Germany. The trophic position and stable isotope ratios of Yellow Perch and European Perch steadily increased with total body length, but European Perch were consistently feeding at higher trophic positions than Yellow Perch at a given length. European Perch occupied considerably higher trophic positions (mean trophic position = 3.9) than Yellow Perch (mean trophic position = 2.8). Large European Perch were increasingly piscivorous, whereas large Yellow Perch were more opportunistic and omnivorous predators of invertebrate prey. Overall, the trophic position among individual Yellow Perch varied more strongly than in European Perch. We conclude that both species similarly increase in trophic position with size, but the specific size-dependency of both trophic position and resource use varies with taxonomy and local ecological conditions. Thus, body size as a sole measure of trophic position should be considered cautiously when generalizing across populations and species.

Keywords Trophic Ecology • Trophic Position • Stable Isotopes • Perch • Body Size

Introduction

Body size plays a critical role in the structure and function of food webs (Elton 1927; Fullhart et al. 2002). Key ecological factors, such as the number of size-classes, secondary production, the number of possible prey items and trophic position are all positively associated with consumer body size (Romanuk et al. 2011; Woodward et al. 2005). Although, exceptions do exist where trophic positions of fishes are not related to body size (Jennings et al. 2001; Layman et al. 2005). Differences in body size are often more important than taxonomic differences for the feeding ecology of fishes (Woodward and Hildrew 2002). Ontogenetic diet shifts with body size are a widespread phenomenon within species, particularly for fishes (Werner and Gilliam 1984). They occur in response to extrinsic environmental factors (e.g., habitat, food supply, predation risk) and organism-specific, intrinsic attributes (e.g., anatomical structures, behavior, physiological demands; de Roos et al. 2002; Persson and Greenberg 1990; Svanbäck and Eklöv 2002). The average size during ontogenetic diet shifts can also differ substantially between populations as a function of local resource availability and competitive pressure and can even manifest differently within one cohort (Persaud et al. 2012; Yasuno et al. 2012). A largely unresolved question is whether interspecific differences in trophic ecology in relation to body size are greater than intraspecific differences.

The closely related European Perch *Perca fluviatilis* (EP) and the North American Yellow Perch *Perca flavescens* (YP) provide a powerful context to systematically describe and compare the size-dependency in trophic position. Native populations of EP are widely distributed from sea level to over 1000 m altitude in Eurasia, whereas YP occur over the same altitudinal range but exclusively in North America (Thorpe 1977). In addition to their shared phylogeny, EP and YP exhibit a high degree of similarity in morphology and physiology (Song et al. 1998; Thorpe 1977). Both species are opportunistic consumers of crustaceans, insect larvae and small fish (Keast 1977; Persson 1983), and exhibit individual specialization in resource use (Ansari and Qadri 1989; Svanbäck and Persson 2004). Stomach and stable isotope analyses in both species have shown that individuals undergo pronounced size-dependent niche shifts from zooplanktivory to benthivory to piscivory (Graeb et al. 2006; Hjelm et al. 2000). Both species are considered facultative piscivores that exploit fish prey late in their ontogeny after having reached a particular size threshold (Mittelbach and Persson 1998). Due to cannibalism and invertivory, both EP and YP can persist even in the absence of other prey fish species (Huss et al. 2013; Knight et al. 1984). Given the complex trophic ecology of perch, it is unknown whether differences in the size-dependency of the trophic positions between these highly similar species exceed the magnitude of variability observed within species.

Diet shifts of strikingly similar fishes so far have rarely been compared between allopatric species of similar morphology and physiology. Such comparisons at the species level can reveal significant differences in the feeding ecology of species or populations in their native and introduced ranges and as a function of local environmental conditions (Brandner et al. 2013; Budy et al. 2013). The objective of the present study was to explore the changes of trophic ecology, indexed by isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), with increasing fish length in six comparable natural lakes in Europe and North America in EP and YP. Furthermore, for a direct comparison of the species, we calculated the trophic position (TP) of individuals across all lakes, and plotted it against fish length as a measure for body size. The TP, representing an energy-weighted mean path length from basal resources to consumers (*sensu* Vander Zanden and Rasmussen 1999), suggests the average consumer level in the food chain. Accordingly, changes in TP with fish length suggest changes in consumer level and hence ontogenetic diet shifts in the two species. As a reference for TP of apex fish predators, we included data for Largemouth Bass (*Micropterus salmoides*) in North American and for Northern Pike (*Esox lucius*) in German lakes. Finally, we used stable isotopes to estimate the contribution of zooplanktonic, benthic and fish resources to the diet of both species. Stable isotopes provide a powerful currency to compare the ecological role and describe the ontogenetic diet shifts of fishes within food webs (Vander Zanden and Rasmussen 1996). We hypothesized that the size-dependent shifts in stable isotopes, trophic position and contribution of prey resources would be similar for YP in the northwestern U.S. lakes and for EP in eastern German lakes.

Methods

Study sites

We examined the realized foraging niches of EP and YP in each of three small (< 0.7 km²), forested and mesotrophic lakes in both eastern Germany and northwestern United States (Table 1). The EP originated from northeastern European lowland lakes in the Schorfheide Biosphere Reserve, situated about 80 km north of Berlin. At the time of the study, the shoreline of Lake Väter and Lake Dölln were surrounded by dense reed belts (*Phragmites australis, Typha latifolia, T. angustifolia*), while Lake Wucker had a steeper slope and less dense reed belts. Submerged macrophytes covered about a third of the littoral zone in Lake Väter and Lake Dölln (mainly *Potamogeton spp.*, *Ceratophyllum spp*., *Najas spp*., *Myriophyllum spp.*) and less than a quarter of Lake Wucker. The most dominant fish species were EP and Roach *Rutilus rutilus* and the most common predatory fish of the lake was Northern Pike. A detailed species list of the fish communities (with catch per unit effort (CPUE) as abundance indicators) and invertebrate orders and families that were identified in each of the lakes is provided in Supplement 1. The lake sediments comprised mainly sand and clay, assembled by terminal moraines during the glacial origin of the lakes. The YP-lakes were located in the Puget Sound lowlands of Washington State, U.S.A. The YP are not native to this region but, together with many other warmwater species of the families Centrarchidae, Esocidae and Ictaluridae, are longtime residencies of these ecosystems, having been introduced in the late 1800s (WDFW 2005). These lakes resembled other lakes within the native range of YP in respect to most physical and habitat characteristics (Brown et al. 2009; Drake and Pereira 2002). Shorelines of Wilderness Lake, Padden Lake and Walsh Lake included scattered canopies of native evergreen and deciduous trees, as well as infrequent occurrence of open space, ornamental gardens (only Lake Wilderness) and non-native shrubs. Littoral zones contained complex habitats characterized by coarse woody debris and both submerged and floating-leaved macrophytes that included pondweeds (*Potamogeton spp.*), non-native pond lilies (*Nuphar spp*.) and plant-like algae (*Chara spp*.). The most dominant fish species was YP and the most common predatory fish of the lake was Largemouth Bass. The lake sediments were characterized by glacial till, an accumulation of clay and boulder, and areas of sandy gravel outwash. Lakes were sampled between July-August (U.S.A.) and October-November (Germany) in 2012. The six study lakes were as similar as possible in trophic status and can be described as being small, mesotrophic, and thermally-stratified during the summer months.

Data collection

Lakes were divided into four quadrants (according to cardinal directions) to distribute sampling effort evenly in space. Littoral prey fish, benthic invertebrates, and zooplankton were sampled to estimate prey isotopic signatures. We sampled a broad range of perch size classes within each quadrant, and sampled the littoral to profundal benthos of the lake with several sampling gears, including minnow traps (41 cm, two 2.54 cm openings and 6.4 mm mesh size) and hoop nets (0.76 m diameter, 7.92 m wing length and five hoops with 24.52 cm² openings) in the U.S.A., hook and line (lure fishing) in the U.S.A. and Germany, electrofishing (Bretschneider Spezialelektronik, Typ EFG

4000, power output: 4 kW, ring anode 40 cm) in Germany and multi-mesh, pelagic gillnets (U.S.A.: 58.52 m x 1.83 m; six panels each 9.75 m long with mesh-sizes 25.4, 31.75, 38.1, 50.8, 63.5 and 76.2 mm stretched mesh & Germany: 30 m x 1.5 m; twelve panels each 2.5 m long with mesh-sizes 5, 6.25, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43 and 55 mm; Lundgrens Fiskredskapsfabrik, Stockholm, Sweden). Perch and prey fish were identified to species and measured for total length (L_T) to the nearest millimeter. Benthic invertebrates were sampled from two randomly selected locations within each quadrant to account for the spatial variability of isotopic signatures of immobile benthic invertebrates (Syvaranta et al. 2006). Invertebrates were collected in different littoral microhabitats (macrophytes, sand, stones, and woody debris), with a D-frame aquatic net (500 µm mesh size) and were also hand-collected from wood and stones. Zooplankton was caught using four oblique tows with plankton nets (100 µm mesh). All samples were put on ice for transport and frozen within 8 hours of collection at -20 °C prior to preparation for stable isotope analyses.

Sample processing

Consumer isotopic signatures reflect those of their prey, and as fish feed at successively higher trophic levels, their $\delta^{13}C$ and $\delta^{15}N$ signatures equilibrate with the isotopic signatures of new prey sources over time (Peterson and Fry 1987). A sudden increase in $\delta^{15}N$ with size is often related to a transition to consuming fish in facultative piscivores (Post 2003). Stable isotopes can thus be used to determine the trophic positions (TPs) of consumers (Post 2002; Post 2003). Accordingly, the TP inferred from $\delta^{15}N$-values increases with size and the exploitation of fish prey in piscivorous fish (Vander Zanden et al. 1997). Moreover, the relevance of littoral-zone resources inferred from $\delta^{13}C$-values also increases with size when C^{13}-enriched benthic prey or littoral fish are included in the diet (Quevedo et al. 2009). Stable isotope mixing models ultimately allow estimating the contributions of specific prey items to fish diets at different stages of ontogeny (Parnell et al. 2013).

The size range of sampled YP (n = 54) included fish from 63 to 267 mm L_T, whereas EP (n = 82) were larger and ranged from 62 to 402 mm L_T. We used white, dorsal muscle tissue, which has low isotopic turnover in comparison with other tissues, of YP from Lake Padden (n = 20), Walsh Lake (n = 19) and Lake Wilderness (n = 15); EP from Lake Dölln (n = 32), Lake Väter (n = 30) and Lake Wucker (n = 20) and of potential prey fishes (Prickly Sculpin *Cottus asper* in the USA and Roach in Germany) for stable isotope analysis (Pinnegar and Polunin 1999). The prey fish were chosen among most abundant fish species in the respective lakes and they had to be small enough to be consumed by perch (L_T < 100 mm). We also determined values for apex predators in all lakes (Pike (*n* = 20) between 169 – 652 mm in the German lakes and Largemouth Bass (*n* = 15) between 87 – 323 mm in the American lakes). Fish were thawed, weighed to the nearest 0.01 g wet weight, and a skinless cube of the dorsal muscle was removed with a scalpel. Zooplankton samples were sorted into groups of Cladocera, Calanoida, Cyclopoida, and *Chaoborus spp.* due to their different TP (Matthews and Mazumder 2003). All other predatory zooplankton (e.g., *Epischura*) and extraneous materials were removed from the samples. Invertebrates were identified and sorted under a dissecting microscope. We pooled invertebrate individuals as necessary to achieve sample target weights. Single individuals were used per sample only for very large taxa (e.g., Anisoptera larvae). All samples were put into aluminium trays, dried for 24 h at 60 °C and ground to a fine powder. Samples were analyzed for carbon ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) by the University of California, Davis Stable Isotope Facility, USA, using a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were compared to in-house laboratory standards calibrated against Vienna PeeDee Belemnite for carbon and air for nitrogen. The measurement error reported by UC Davis is the longterm standard deviation of 0.2 ‰ for $\delta^{13}C$ and 0.3 ‰ for $\delta^{15}N$. We report stable isotope values in standard delta notation,

$$\delta^{H}X = [(R_{sample} / R_{standard}) - 1] \text{ x } 10^3,$$

where *X* is the element, *H* is the mass of the heavier isotope, and *R* is the ratio of the heavy to light isotope in the sample and standard. The δ-value measures the amount of heavy and light isotopes in a sample. $\delta^{13}C$-values were not corrected for lipids because lipid normalization works poorly on invertebrates (Kiljunen et al. 2006) and perch dorsal muscle exhibits low lipid contents and low C:N-ratios (Mackintosh et al. 2012).

Stable isotope analysis

Trophic positions (TPs) of individual perch were calculated per lake according to Post (2002) to achieve a comparable measure for TP that takes into account the habitat and lake specific ^{15}N-^{13}C relationships within lentic systems (Vadeboncoeur et al. 2002):

$$TP_{\mathrm{c}} = \lambda + (\delta^{15}N_{\mathrm{c}} - [\,\delta^{15}N_{\mathrm{base1}} \times \alpha + \delta^{15}N_{\mathrm{base2}} \times (1-\alpha)])/\Delta^{15}\mathrm{N}.$$

Here, $\delta^{15}N_c$ is the measured $\delta^{15}N$-value of the consumer (c), for which TP should be estimated (i.e., EP or YP). The parameters $\delta^{15}N_{base1}$ and $\delta^{15}N_{base2}$ are the measured $\delta^{15}N$-values of the baseline organisms chosen to represent littoral (base1 = Gammaridae; USA or Asellidae; Germany) and pelagic food webs (base2 = Cladocera) of each lake. Gammaridae were found in all American lakes but in only one German lake, and were isotopically very similar to Asellidae, which were abundant in German lakes. The λ represents the estimated TP of baseline organisms ($\lambda = 1.5$ for primary consumers), selected based on values from the literature (Solomon et al. 2011) The ratio of the different reaction rates for the light and heavy isotopes was expressed as the fractionation factor ($\Delta^{15}N = 3.4‰$). The contribution of each food web component (α) to the consumer signature was estimated using carbon isotopes ($\delta^{13}C$) such that:

$$\alpha = (\delta^{13}C_{consumer} - \delta^{13}C_{base2})/(\delta^{13}C_{base1} - \delta^{13}C_{base2}).$$

Because lakes are typically characterized by a pelagic (1-α) and littoral food web (α), α denotes the proportion derived from each of these sources (see Post 2002). The parameters $\delta^{13}C_{base}$ and $\delta^{13}C_{consumer}$ are the measured $\delta^{13}C$-values of the baseline organisms and consumers.

Stable isotope mixing models were used to illustrate the TP of EP and YP and study differences in foraging niches between size classes. The perch were grouped into two size classes (< 150 mm vs. > 150 mm – 270 mm) according to studies on ontogenetic diet shifts to piscivory (Mittelbach and Persson 1998). Potential prey sources of each size class within each lake were modeled separately with a Bayesian mixing model implemented in the R package *SIAR* (Stable Isotopes Analysis in R, Ver. 4; Parnell et al. 2010). Isotopic biplots (Supplement 2 & 3) were checked for abundant, potential prey items, which represented typical benthic and pelagic food items with respect to published dietary data of perch. To minimize effects of differing size ranges between the European and American samples, only perch up to $L_T = 270$ mm were included in the mixing model.

In German lakes, the following groups were included in the mixing model: Asellidae/Gammaridae, zooplankton (Cladocera, Calanoida, Cyclopoida), Spinycheek Crayfish *Orconectes limosus* (only for EP > 150 mm L_T) and Roach (only for EP > 150 mm L_T). We included crayfish in the analyzed lakes because previous studies have shown that crayfish was a highly important food item for EP, especially in Lake Väter (Haertel Borer et al. 2005; Schulze et al. 2012). However, we were unable to sample crayfish in the other lakes given their low abundance. Probably due to flooding events at the time of sampling, which made shallow parts of the lake inaccessible for trapping, and maybe due to a recent increase in the European Catfish *Silurus glanis* population in Lake Dölln, no crayfish were caught in Lake Dölln and Lake Väter. Only dead crayfish were observed during benthic sampling in these lakes. In the American lakes, we included the groups Asellidae/Gammaridae, zooplankton (Cladocera, Calanoida, Cyclopoida), Signal Crayfish *Pacifastacus leniusculus* (only for YP > 150 mm L_T) and Prickly Sculpin (only for YP > 150 mm L_T). In Lake Walsh only one juvenile crayfish was caught, which was not included in the analysis.

Mean δ^{13}C- and δ^{15}N-values and standard deviations of all samples per group were computed and included in the model (Supplement 4). The mean fractionation factors were 3.4 (SD = 1.0) for nitrogen (Post 2002; Vander Zanden and Rasmussen 2001) and 1.13 (SD = 0.80) for carbon (Vander Zanden and Rasmussen 2001). The carbon to nitrogen (C:N) ratio, given by the amount (µg) of carbon and nitrogen in the sample (i.e., concentration dependence), for all samples was included in the model. Three small perch from Lake Wilderness were outside the convex hull implied by the (dietary) sources and were excluded from the mixing model as outliers. No models were calculated for small YP in Walsh Lake (*n* = 0), small EP in Lake Wucker (*n* = 1) and large YP in Lake Wilderness (*n* = 2) because of limited sample size. The outputs for each lake were given as mean proportion of potential prey sources.

Statistical analysis

We calculated linear regressions between body size and stable isotope signals for each fish species and lake with L_T as the predictor variable, and stable isotope values (δ^{15}N and δ^{13}C-values) as the response variables. A positive correlation of L_T and δ^{13}C is indicative of a shift from a mixed pelagic–benthic diet to a primarily benthic diet depending on decreasing isotopic turnover in large fish (Vander Zanden et al. 1998). In turn, negative correlations suggest higher reliance on autochthonous energy sources (Weidel et al. 2008). A positive correlation of L_T and δ^{15}N suggests an increase in trophic position (Post 2002). Linear regressions were calculated in SPSS (IBM SPSS Statistics for Windows, Ver. 21.0.).

To increase sample size for the regressions and TP-analysis, we added TP-data of YP (*n* = 11) and Largemouth Bass in Walsh Lake (*n* = 15) and YP in Lake Wilderness (*n* = 3) from 2009 (Julian Olden, University of Washington, unpublished data). The δ^{13}C- and δ^{15}N-values of benthic crustaceans (Asellidae & Gammaridae) and zooplankton from 2009 and the present dataset (2012) were compared via Student's t-test. When prey items did not differ significantly, the TP of YP was calculated and implemented into the data set.

We tested whether the slope of the regression between TP and length differed between the species, by running an ANCOVA with species as the fixed factor and L_T included as covariate in R (command anova; R Ver. 3.4.0.). A significant interaction term (species × total length) would suggest that TP changes with length differently between the species. Only perch $L_T \leq 270$ mm were included in the models to account for size disparity among samples. Model significance for statistical analyses was assessed at $\alpha = 0.05$.

Results

In EP, δ^{13}C and δ^{15}N signatures increased with body length (Figure 1). Five out of six regressions were significant, and the sixth showed a strong trend. However, the largest EPs ($L_T > 300$ mm) that were caught were more depleted in ^{15}N and more enriched in ^{13}C than intermediate sized fish (particularly in Lake Väter & Lake Wucker). In contrast, δ^{13}C and δ^{15}N signatures did not increase systematically with body length in YP (Figure 2). Only two (δ^{15}N in Lake Wilderness and δ^{13}C in Lake Padden) out of the six L_T - isotopic signature regressions were significant, and the relationship between δ^{13}C and L_T for YP was even negative in Lake Padden.

Trophic position corrected for length differed between the species. The TP increased with body length for both species (Figure 3, Table 2), but the slope of the TP-L_T regression was lower for YP than for EP (interaction term species × L_T, df = 1, $t = -2.07$, $P = 0.04$, Table 2). The model showed that the intercept of TP of both species differed by 0.90 (df = 1, $t = -5.52$, $P < 0.001$). The TPs in YP ranged from 1.97 ($L_T = 127$ mm, Lake Wilderness) to 3.38 ($L_T = 120$ mm, Lake Padden) and were in average at 2.77 ± 0.35. Trophic positions calculated for EP ranged between 3.12 ($L_T = 80$ mm, Lake Wucker) and 4.86 ($L_T = 379$ mm, Lake Väter) and were in average at 3.90 ± 0.34. Pike (between 169 – 652 mm) in the German lakes exhibited similar trophic positions as large European perch (Supplement 2). Largemouth bass (between 87 – 323 mm) mostly had higher TPs than YP (Supplement 3).

Potential prey sources, as estimated from isotopic mixing models, strongly differed between the species (Figure 4). Small YP utilized higher proportions of zooplanktonic resources, while small EP utilized benthic resources, like gammarids and asellids. For large YP, high contributions of zooplanktonic and benthic resources were found, while for large EP, prey fish were more important. The position of all perch in the isotope biplots ranged from half a trophic level up to almost three trophic levels above the trophic level of invertebrates (Supplement 2 & 3). Pike exhibited similar patterns in the biplots as European perch (Supplement 2). Largemouth bass mostly had higher TPs compared to YP (Supplement 3).

Discussion

In contrast to our assumption, the morphologically and physiologically strikingly similar EP and YP displayed strong differences with respect to the length-dependency of trophic positions and major prey sources. Body length was only a weak correlate of TP for YP, whereas this association was considerably stronger for EP. Furthermore, we found evidence for gradual ontogenetic diet shifts for both percid species. Our results support the characterization of EP as an 'ontogenetic omnivore' that switches from benthic organisms to fishes as the dominant prey source for the largest individuals (*sensu* Persson et al. 2000). In contrast, we found little evidence for a diet shift and minor importance of piscivory in the studied YP populations. These results suggest that these two perch species may play different functional roles in the food webs of lakes.

For EP, our calculated TPs and mixing model results strongly supported a transition from an invertebrate diet to a piscivorous diet with increasing body length. Large proportions (> 40%) of fish prey were estimated for large EP > 150 mm length. Here we focus only on the second diet shift of EP from benthivory to piscivory because we examined only fish with body lengths > 60 mm, which may have completed the shift form zooplankton to benthic diet already at smaller sizes (Graeb et al. 2006; Wahlström et al. 2000). The high TPs of large EP (max. TP = 4.96) suggest that EP can take a position high up in the food chain when prey fish are abundant (Dörner et al. 2003; Mittelbach and Persson 1998). Large EP have a gape width large enough to be able to feed successfully on prey fish (Dörner et al. 2003). Previous studies suggest that fish are the primary prey item of EP, which exceed a size threshold of about 110-160 mm L_T (Mittelbach and Persson 1998). A high TP of EP within the food web of the studied systems was emphasized also by our finding that obligatory piscivorous pike and large EP had similar TPs and similar positions in isotopic biplots. Therefore, large EP seem to successfully compete with pike for prey fish, likely because perch use the open water and the sublittoral and pike are bound to the littoral (Kobler et al. 2009; Nakayama et al. 2016). The set of prey species available in German lakes allows for specialization of pike and perch on certain prey species, facilitated by habitat segregation (Vander Zanden et al. 1999a). The catch per unit effort and the high number of cyprinid species in the study lakes indicate that abundance and size variability of potential prey species might favor piscivory and high TPs in EP.

In contrast to EP we found low TPs and a high contribution of invertebrates to the estimated diet. Compared to some YP populations from their native range the studied populations were less piscivorous (e.g. Barks et al. 2010; Fullhart et al. 2002). Food habits and prey preferences can differ between populations from the original area of distribution and the invaded range (Brandner et al. 2013; Budy et al. 2013). In Largemouth Bass, for example, piscivory was found to be lower outside its native range (García-Berthou 2002). However, we found many different species that co-occur in the native range of YP and in the Washington lakes, especially centrarchids. Thus, the community did not differ much from many lakes in the native range. All American lakes also had Largemouth Bass that compete with YP for prey (Clady 1974). Largemouth Bass had a higher TP and occupied a higher level in the isotopic biplots in our study lakes. Largemouth Bass might represent an important predator of the few small fish prey available in the American study lakes, which forces YP to rely more on benthic resources (Twardochleb and Olden 2016).

The benthic living Prickly Sculpins sampled in American lakes could have been an important fish prey for YP. Stomach analyses and isotope mixing models of YP in Lake Washington, USA demonstrated that large YP (L_T > 225 mm) increasingly consume sculpins (McIntyre et al. 2006), yet other evidence suggests that gape-limited YP often choose smaller fish prey than predicted by gape size (Truemper and Lauer 2005). Studies on the piscivory of YP emphasize the importance of slender prey fish like Brook Sticklebacks *Culaea inconstans* or Johnny Darters *Etheostoma nigrum* (Fullhart et al. 2002; Knight et al. 1984). Sculpins were not overly abundant, and the most abundant potential prey fish for YP in the study lakes were young centrarchids (Pumpkinseed Sunfish *Lepomis gibbosus*, Green Sunfish *L. cyanellus* and Largemouth Bass), all of them deep-bodied. Also, YP can feed opportunistically on small fish in summer, when these are most abundant (Horppila et al. 2000; Knight et al. 1984). Thus, increased piscivory might also happen seasonally for the populations examined; a pattern which was not detectable based on our sampling regime. Piscivory can further be delayed or interrupted by feeding on large invertebrates (García-Berthou 2002). Unfortunately, comparisons to the functional niches of large YP were limited in the present study because very large YP (L_T > 270 mm) were not abundant enough to be collected and might be limited by population density (Headley and Lauer 2008). Body size has found to be rather unimportant for the TP in omnivorous species (Persaud et al. 2012), and also species that have ontogenetic diet shifts sometimes lack this relationship (Vander Zanden et al. 2000). The patterns we found support the lack of a strong TP-L_T relationship in the studied YP populations and together with modeled diets of YP point towards a flexible, generalist feeding strategy or a high degree of omnivory.

Variability in TP and the reliance of YP on carbon derived in different lake habitats, as indicated by carbon signatures, both were much higher among individual YP than among individual EP within two of the three lakes. The broad range of individual δ^{13}C-signals we found in YP corresponds with other North American studies (Bertrand et al. 2011; Persaud et al. 2012) and suggests a higher degree of individual specialization in foraging among YP compared to EP at the same sizes. The TPs derived from stable isotopes of individual fish represent a time-integrated measure of individual diet differences (Beaudoin et al. 1999). Individual resource use and bimodality in resource use have been well studied in EP (Svanbäck and Eklöv 2002; Svanbäck and Persson 2004; Svanbäck et al. 2015) but have rarely been studied in YP (Parker et al. 2009).

Generally, the range of calculated TPs in our study was within limits determined for other perch populations (Bertrand et al. 2011; Quevedo et al. 2009). The average TP of EP (3.9) was in a similar range for perch, compared to previous studies (Quevedo and Olsson 2006). By contrast, the average TP of YP was about 2.8, which was substantially lower than that of EP and the TPs calculated for YP by Cabana and Rasmussen (1996). Thus, it can be concluded that already small size classes of both perch species within the studied communities realize different foraging niches, with EP feeding higher in the food chain compared to YP. This finding likely reflects the different TPs of cladocerans and asselids or gammarids within the European and North American food webs (Supplement 2 & 3). We do not have data on the exact TP of primary producers, and hence a mechanistic explanation for the TP differences of primary consumers requires additional investigation. Differences in food chain length might have biased the calculations of perch between the German and the Washington Lakes (Vander Zanden et al. 1999b). However, we tried to choose similar systems where we found similar functional groups and consider the food chains to be similar as well. A more important element of uncertainty in our calculations is the choice of fractionation factor. The estimate from Post (2002) has been widely adapted for stable isotope models of fishes but might be inaccurate for one or even both systems since different diet isotopic values have been shown to result in different discrimination factors (Caut et al. 2009).

Looking at the overall patterns, we found that stable isotopes as well as TP tended to level off at larger L_T. Since the two perch species are so similar in almost all aspects of their ecology and especially because they exhibit relatively distinct ontogenetic shifts, we suspected to see similar patterns in both species. However, patterns in stable isotopes, can be skewed, for example, by mobile predators which link different food webs (McCann et al. 2005; Rooney et al. 2006). Also, body size does not necessarily determine the trophic level that a species feeds at (Jennings et al. 2001). The very large EP (L_T > 270 mm) from the studied lake systems may feed intensively on crayfish, as indicated by an increasing ^{13}C-value with body length and diet estimates. This would be in agreement with previous work in the study lakes and explain why TP flattens out in the very large EP (Haertel Borer et al. 2005; Schulze et al. 2012). Abundant prey of a low trophic order such as snails might have influenced the pattern of YP. For example, Chinese mystery snails (*Bellamya chinensis*) have been found in YP stomachs of several lakes in the region (Twardochleb and Olden 2016). If larger consumers feed on prey of a low trophic order there would be a flattening or a more hump-shaped relationship between body size and TP as suggested by Arim et al. (2007).

Different size preferences of the consumer (i.e. larger consumer prefer smaller prey) or large prey items of a low trophic order (like in crayfish) can skew body size – TP relationships and have to be considered when looking at diet shifts with stable isotope-based parameters (Arim et al. 2010). For example, pelagic prey fish of lake trout (*Salvelinus namaycush*) did not have a positive TP-L_T relationship (Vander Zanden et al. 2000) As long as small consumers are strongly gape-limited, the relationship is positive and TP increases with body size, while the maximum TP of larger consumers decreases as metabolic demands (set by temperature) increase (Arim et al. 2010; Arim et al. 2007). Such a hump-shaped pattern of body length and stable isotopes was found, for example, in the ontogenetic shift of the cichlid species *Pseudotropheus callainos* (Genner et al. 2003). We cannot test the community-based hypotheses of Arim et al. (2007) that energetic limitations constrain the TPs in larger consumers, but some of the patterns we found in δ^{15}N-signals of perch declining towards the larger end of the size spectrum (e.g., Figure 1c, 1e and maybe also 2e) could be interpreted this way.

Our results show that intraspecific differences in YP exceed the magnitude of variability between YP and EP. Other studies on TP - body size relationships in fishes showed that interspecific shifts at the community level are usually stronger than TP-shifts with body size at the species level (Jennings et al. 2001; Persaud et al. 2012). However, ontogenetic shifts can evoke strong TP - body size relationships also at the species level (McIntyre et al.

2006; Yasuno et al. 2012). Small predators are often limited in what prey they can consume, and niche overlap with other species and conspecifics usually declines with an increase in body size (Woodward and Hildrew 2002). Weaker TP-L_T relationships should be an attribute of more omnivorous species and stronger relationships mainly connected to piscivorous feeding habits. In a meta-analysis over several orders of fish species, Romanuk et al. (2011) found a positive relationship between body size and trophic level for 3,822 species of the order of Perciformes combined. They found the strongest correlations in orders with relatively small average sizes and adaptation counteracting gape-limitation. These traits also apply to EP and YP, which are both small predators with a protrusible mouth, but our data indicate piscivory was mainly confined to EP and less present in the YP we studied.

In conclusion, both species exhibited differences in the increase of TP with L_T. Ontogenetic diet shifts among the two percids still might follow species-specific patterns. However, the small scope of our study does not rule out lake-specific ecological effects or some level of sampling artifacts. Size-dependency of the TPs seemed to be more variable within YP than they were between YP and EP. Our results showed a clear increase in TP and ^{13}C with size for EP, but no such clear ontogenetic shifts were present in the YP we sampled. In the studied lakes, large-bodied individuals of YP seemed to be more omnivorous, whereas EP seemed to be largely piscivorous, which questions simple rules of size-based trophic structuring. Certainly, the number of lakes included in this inter-continental study is not sufficient to definitely answer the question of ecological equivalence between YP and EP originally proposed by Thorpe (1977). The abundance and composition of prey items and predators among the lake ecosystems might co-explain the patterns we found, and thus our results might not hold true for other ecosystems not sampled in our work. We would encourage future global compilation of results from single-lake studies, to conduct a synthetic comparison of potential differences in ontogenetic diet shifts of YP and EP. In particular, the size-dependency of foraging should be examined for lakes of different food chain lengths and top-down interactions within communities, to determine whether our results are broadly transferable to lakes outside of eastern Germany and northwest United States.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of Interest: The authors declare that they have no conflict of interest.

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Tables

Table 1 Location, size, maximum depth (Z_{max}), Secchi depth (m) and phosphorus concentration (T_P) of the studied lakes, measured in June and July 2012 in North America (USA) and October and November in Europe (Germany, GER). The total phosphorus concentration (T_P) is the result from a mixed sample of one epi- and one hypolimnetic water sample per lake

Lake	Lat. (dec. °)	Long. (dec. °)	Altitude (m)	Surface Area (km^2)	Z_{max} (m)	Secchi (m)	T_P (µg/l)
USA							
Padden	48.7027	-122.4529	137	0.64	18.0	3.2	23
Walsh	47.4085	-121.9285	221	0.24	10.7	3.2	11
Wilderness	47.3726	-122.0344	143	0.28	11.6	3.2	16
Germany							
Dölln	52.9946	13.5818	54	0.25	7.8	1.8	33
Väter	53.0051	13.5530	60	0.12	11.5	2.2	22
Wucker	53.0071	13.6424	64	0.22	16.1	3.8	14

Table 2 ANCOVA results testing for differences between trophic positions (TP) and species (*P. fluviatilis* (EP) and *P. flavescens* (YP); $r_2 = 0.80$ (adj. $r_2 = 0.80$)) with total length (L_T) as a covariate (SS = sum of squares, df = degrees of freedom, MS = mean square, *F* = F-statistic, *P* = p-value).

Source	SS	MS	df	*F*	*P*
species	40.22	40.22	1	458.23	< 0.001***
L_T	3.81	3.81	1	43.40	< 0.001***
species × L_T	0.37	0.37	1	4.26	0.04*
residuals	10.80	0.09	123		

Figures

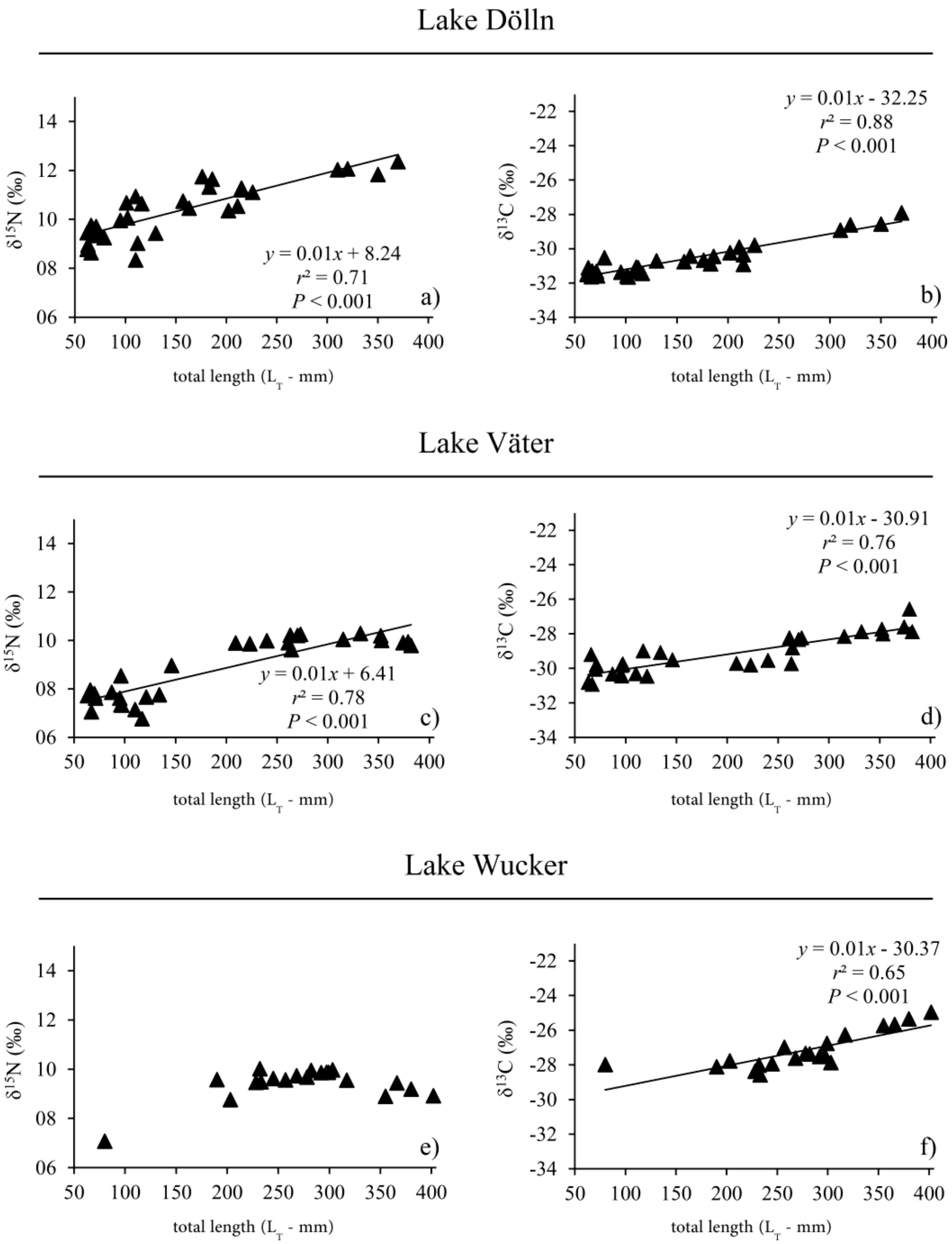

Fig. 1 Scatter plots (triangles) and significant linear regressions (lines) between isotopic signatures (δ^{15}N and δ^{13}C) of muscle tissue from *P. fluviatilis* (EP) and total length (L_T) in Lake Dölln (a & b), Lake Väter (c & d) and Lake Wucker (e & f). Black triangles represent samples from individual EP

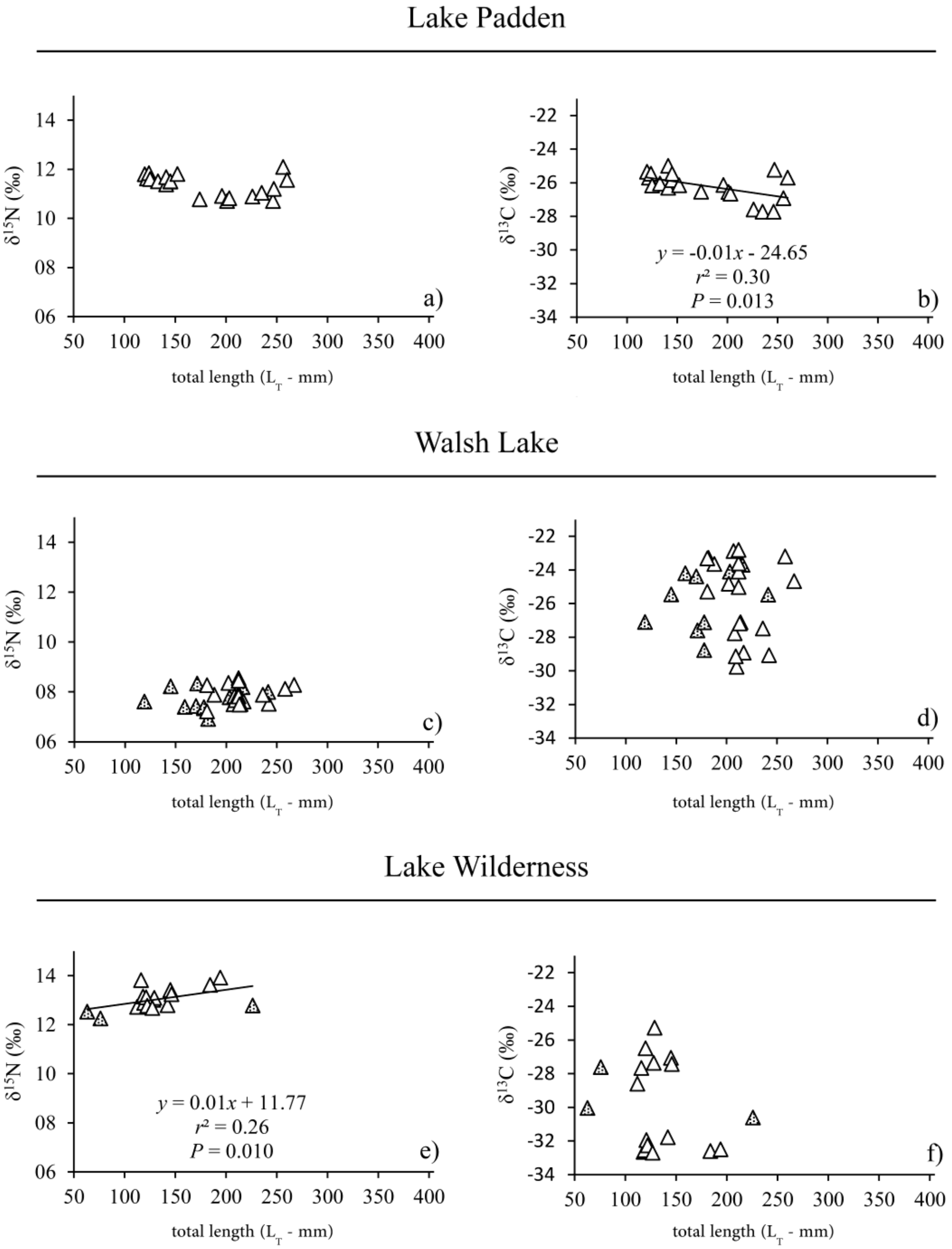

Fig. 2 Scatter plots (triangles) and significant linear regressions (lines) between isotopic signatures (δ^{15}N and δ^{13}C) of muscle tissue from *P. flavescens* (YP) and total length (L_T) in Lake Padden (a & b), Walsh Lake (c & d) and Lake Wilderness (e & f). Unfilled triangles represent samples from individual YP caught in 2012 and dotted triangles are YP from the 2009 dataset (Julian Olden, unpublished data)

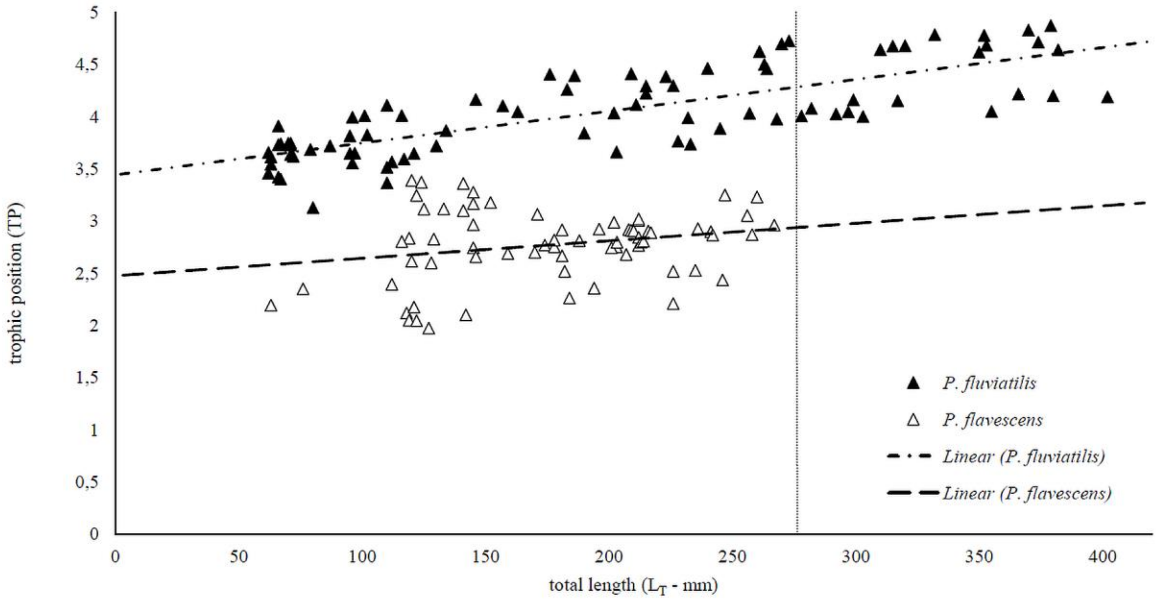

Fig. 3 Trophic positions (TP - i.e., the average position relative to primary producers at which an organism feeds) of *P. flavescens* (YP- unfilled triangles) and *P. fluviatilis* (EP- black triangles) at increasing total length for all lakes combined. The significant linear regressions are shown as dotted (YP) and dashed (EP) lines

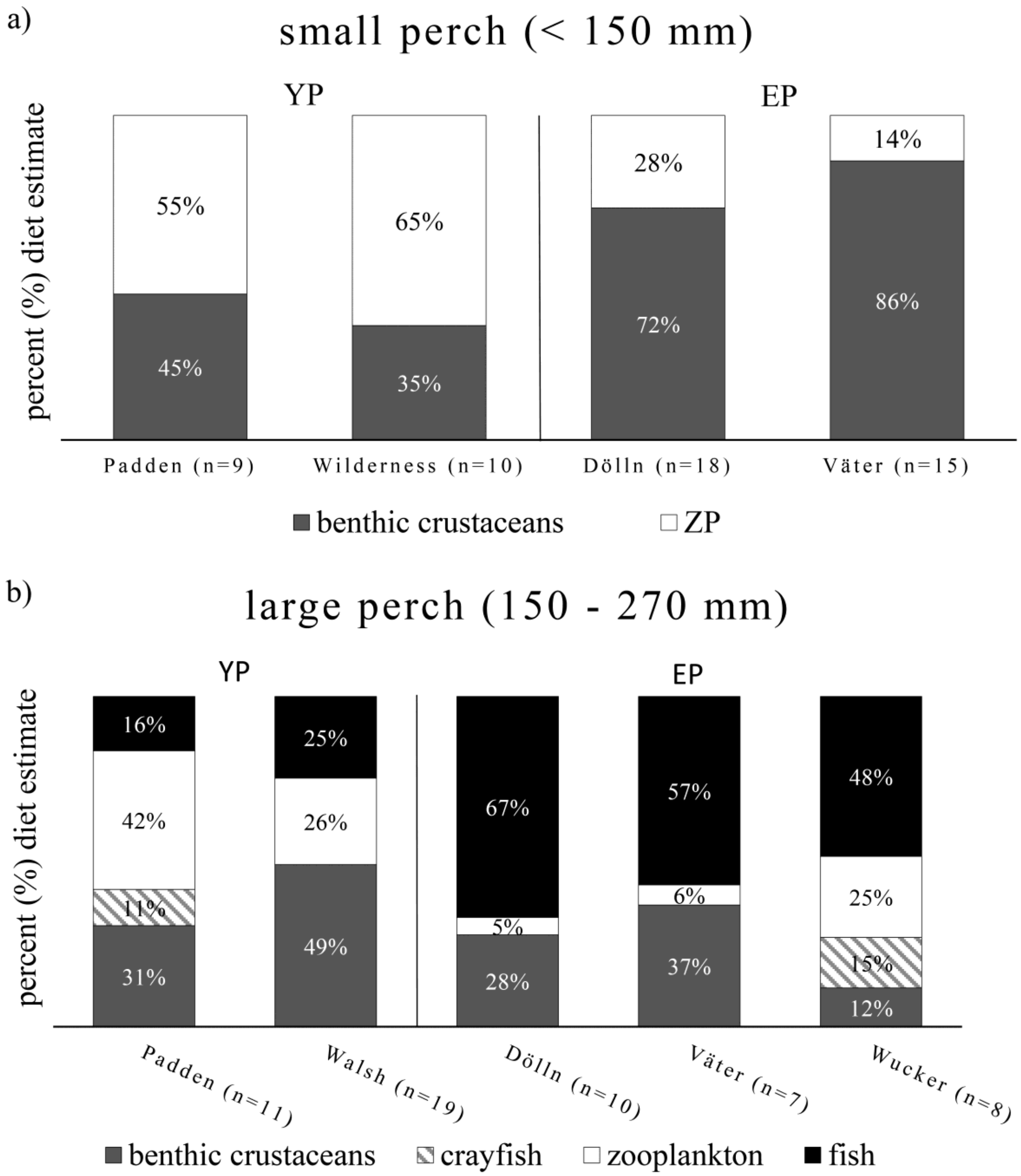

Fig. 4 Results of the SIAR (stable isotope analysis in R) mixing model of mean diet estimates in percent (%) of zooplankton (light grey), benthic crustaceans (Gammaridae/Asellidae – grey), crayfish (dashed, dark grey – for large only) and fish (black – for large only) for small (a, $L_T < 150$ mm) and large (b, $L_T = 150$ mm – 270 mm) *P. flavescens* (YP) and *P. fluviatilis* (EP) for single lakes, inferred from stable isotopes. Sample size (*n*) is given in brackets. Sample size for small YP from Lake Walsh, small EP from Lake Wucker and large YP from Lake Wilderness were too limited to be evaluated.